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A REVISED INTERPRETATION OF THE PRIMITIVE
CENTIPEDE GENUS *ARRUP*, WITH REDESCRIPTION
OF ITS TYPE-SPECIES AND LIST OF KNOWN SPECIES¹
(CHILOPODA : GEOPHILOMORPHA : MECISTOCEPHALIDAE)

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In 1912 (p. 654), Chamberlin proposed a new genus and species, *Arrup pylorus*, creating for its reception a new family, Arrupidae. In 1920 (p. 184), he reduced Arrupidae to the rank of subfamily within Mecistocephalidae, where it properly remains today.

This genus, represented apparently only by the original species, had long puzzled me. Quite clearly it seemed very similar to the eastern Asian *Prolamnonyx*, but according to the original description of *Arrup*, there was a major intra-generic difference between the two. In *Prolamnonyx* the first maxillary coxosternum is entirely without midlongitudinal division, whereas according to Chamberlin's characterization of *Arrup*, the first maxillary coxosternum is distinctly sutured or divided midlongitudinally (see 1912: 667, Fig. D). The types could not be located, and until quite recently additional specimens of *pylorus* could not be found.

Some years ago a Californian chilopod collection made by R. O. Schuster and L. M. Smith was generously placed in my hands by my friend and colleague, Dr. R. L. Hoffman. Recently, while continuing my perusal of this material, I unexpectedly came upon seven specimens of a genus that I unhesitatingly identified at first as *Prolamnonyx*. Generically they agree in every detail with all of the *Prolamnonyx* speci-

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mens that I have seen, including the holotype of the type-species, *holstii* (Pocock), which I had examined in the British Museum (Natural History). Then two discoveries led me to believe that these specimens are in fact referable to *Arrup pylorus*.

First, although in every specimen the first maxillary coxosternum is absolutely entire and has no true midlongitudinal suture or other division, in one specimen the coxosternum is slightly infolded midlongitudinally, grossly giving the erroneous impression that it is divided or suturate. The illusion is further strengthened by the underlying, seemingly divided musculature, which, when viewed by transmitted light, suggests a nonexistent midlongitudinal division. In no specimen is there a true midlongitudinal division such as is seen in all other mecistocephalid genera. In each specimen the areolation is continuous from one side of the coxosternum to the other.

Secondly, apart from this maxillary character, it is apparent that these specimens agree in every other detail with the original description of *Arrup pylorus*. This centipede is bizarre even among the Mecistocephalidae, and in North America it is quite unlike anything else that is known. Therefore I submit that the original description of *pylorus* was in error, and that its first maxillary coxosternum is actually nonsuturate and undivided.

It follows that since *holstii* (Pocock), the type-species of *Prolamnonyx* Silvestri, 1919 (by original designation), is held to be congeneric but not conspecific with *pylorus* Chamberlin, 1912, the type-species of *Arrup* Chamberlin, 1912 (by original designation and monotypy), that *Prolamnonyx* falls as a junior subjective synonym of *Arrup* (New Synonymy).

Before proceeding to a necessary redescription of *pylorus*, I should like to call attention to another long-accepted genus whose name must fall as a junior synonym of *Arrup*. It is *Nodocephalus* Attems, 1928 (p. 115).

Nodocephalus was proposed for the reception of a single species, *edentulus* (Attems, 1904: 119), which was described from "Przewalsk" = Przheval'sk, Siberia (42° 29' N, 78° 24' E).

I have examined the mouthparts of the holotype in Vienna and find the original description to be in error. Attems' figure 159 (1929: 148)

illustrates the point in question. Both in the text and in this figure he indicates that the second maxillary coxosternum is entire, not sutured, yet the holotype's second maxillary coxosternum is very distinctly sutured midlongitudinally. Other characters as well suggest a very close relationship with *holstii* and *pylorus*. Therefore I conclude, since *edentulus* is congeneric but not conspecific with *pylorus*, that *Nodocephalus* is a junior subjective synonym of *Arrup* (New Synonymy).

The presence of this evidently primitive mecistocephalid genus in central and eastern Asia and on the west coast of North America reflects a familiar distributional pattern with examples in a number of invertebrate groups, one being Chilopoda. The number of chilopod genera known to occur in western North America and eastern Asia is growing steadily, e.g., *Geophilus*, *Brachygeophilus*, *Tomotaenia*, *Strigamia*, *Escaryus*, *Dicellogophilus*, *Arrup*, *Cryptops*, *Scolopocryptops* (*olim Otocryptops*), and a number of lithobiid groups. It seems reasonable to assume that passage between the two continents was effected by migrations across the Bering Strait during interglacial times.

Arrup Chamberlin

Arrup Chamberlin, 1912, p. 654.

Prolamnonyx Silvestri, 1919, p. 47 (key), p. 84 (new synonymy).

Nodocephalus Attems, 1928, p. 115 (new synonymy).

Type species: *Arrup pylorus* Chamberlin, 1912 (monotypic and by original designation). Its possession of a nonsutured, undivided first maxillary coxosternum will distinguish *Arrup* from all other known mecistocephalid genera.

Important Correlative Generic Criteria: Head only slightly longer than wide. Clypeal plagulae completely separated and not more than half as long as entire clypeus. Buccal spiculum absent. Labral sidepieces without setae or filaments on posterior edge. First maxillary coxosternum not divided midlongitudinally. Second maxillary isthmus broadly membranous, not areolate, and infolded or not, thus in effect separating the coxosternites; metameric pore opening posteromesally, bounded laterally by a long foraminal process. Trochanteroprefemur of prehensor without a proximal denticle. Sternital porefields absent. Sternital rhachides anteriorly not furcate, each simply formed by a deep sulcus with thickened walls. Anal pores present and large.

Characters of Arrup and Its Systematic Position: Heretofore unnoted as a valuable intrageneric (if not suprageneric) character are the orientation and structure of the second maxillary metameric pore and adjacent parts. In the vast majority of Geophilomorpha this pore opens mesally or posteromesally and is bounded laterally by the bulk of the coxosternite. I take this to be the primary or primitive condition.

By contrast, in nearly all of the mecistocephalids concurrent with a general elongation of the entire maxillary apparatus, the mesal portions of the coxosternites undergo hypertrophy with the result that they become

extremely elongate posteriorly. As a consequence the lateral portion of each coxosternite atrophies, or tends to, thereby displacing the metameric pore from its original mesal position to a secondary, lateral one. This derivative, lateral orientation is well-illustrated in, e.g., *Mecistocephalus*, *Tygarrup*, and *Anarrup*.

At least in *Arrup*, however, the original pore orientation and basically the original maxillary structure are retained. Interestingly enough, in *Dicellophilus* (western North America, eastern Asia, south-central Europe), we observe what may be a condition intermediate between these two extremes. The mesal parts of the coxosternite are partly elongate, a foraminal process is partly formed, and the metameric pore is partly oriented laterad.

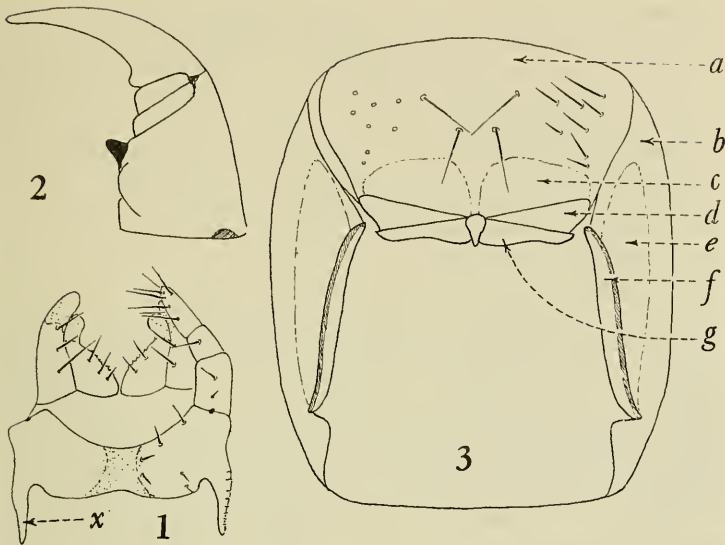
Thus in *Arrup* we see what appears to be only a slightly modified version of the primitive coxosternal condition. The metameric pore opens posteromesally, not laterally, and it is still completely separated from the bucca by the long, thin vestige of the lateral part of the coxosternite. For convenience of designation and to signalize its special significance I shall name this outer coxosternal vestige the *foraminal process*.

The sternal apodemes, which I have previously termed the rhachides (1959: 192, G), also deserve special comment. In *Mecistocephalus*, reflecting a more advanced or more complex habitus than that of *Arrup*, each rhachis is a solid internal extension (through invagination) of the sternite. Depending upon the species, it is anteriorly forked or not. A study of the homologous structure in *Arrup* shows how the more typical rhachis of *Mecistocephalus* must have evolved.

In *Arrup pylorus* and *holstii* each rhachis is represented by a deep midlongitudinal sulcus with thickened walls. Evidently in the course of evolution in order to provide a larger, firmer structure for muscle attachment and support, invagination of the sternal surface continued to form an ever-deepening sulcus which eventually closed over, ultimately giving rise to a solid rod- or fork-like internal apodeme.

In summary, the following features of *Arrup* seem to me to be suggestive of its evolutionary conservatism or primitiveness within the Mecistocephalidae. The head is only slightly longer than wide. The prehensors are shorter and less massive than those of other genera. The prelabral plagulae are entirely separated from each other and are relatively short anteroposteriorly. There is no buccal spiculum. The first maxillary coxosternum is undivided centrally. The second maxillary pore opens posteromesally, not laterally, and has a well-developed foraminal process. The sternal rhachides consist simply of open sulci with thickened walls. Large anal pores are present.

Therefore, I concur with Chamberlin and Attems in their beliefs that *Arrup* is sufficiently distinctive to warrant inclusion within a separate subfamily, Arrupinae, but my reasons for this allocation are different from theirs. I believe that they exaggerate the significance of the second



FIGS. 1-3. *Arrup pylorus* Chamberlin. 1, First and second maxillae; ventral aspect; right telopodite of second maxillae removed; all setae of left sides shown. x = right foraminial process. 2, Left prehensor; ventral aspect; setae deleted. 3, Cephalic capsule; ventral aspect; all setae shown except those of extreme right side of clypeus. *a*, areolate portion of clypeus; *b*, areolate portion of left bucca; *c*, non-areolate portion of clypeus (clypeal plagula); *d*, anterior ala of left labral sidepiece; *e*, non-areolate portion of left bucca; *f*, left buccal stilus; *g*, posterior ala of left labral sidepiece.

maxillary central division, while failing to grasp the classificatory utility and evolutionary implications of two other maxillary features.

First, in possessing an undivided first maxillary coxosternum, *Arrup* differs from all other known members of the family. Secondly, *Arrup* and one other, as yet undescribed, genus, has the maxillary pore posteromesally oriented and laterally bounded by a long, prominent foraminial process. This character-complex, overlooked until now, is a most useful classificatory device but in addition has apparent evolutionary implications.

The Known Species of *Arrup*

1. *A. pylorus* Chamberlin, 1912. (Type-species of *Arrup*.) California.
2. *A. edentulus* (Attems, 1904). (New combination.) Siberia.
3. *A. holstii* (Pocock, 1895). (New combination.) Japan, China.
4. *A. sauteri* (Silvestri, 1919). (New combination.) Formosa.

5. *A. dentatus* (Takakuwa, 1934). (New combination.) Japan.
6. *A. obtusus* (Takakuwa, 1934). (New combination.) Japan. On the basis of the original description, it is not possible to distinguish *obtusus* from *holstii*, with which it may be conspecific.
7. *A. doii* (Takakuwa, 1940). (New combination.) Korea. This species was originally referred to *Nodocephalus*. Its description is very vague and imprecise and, I suspect, may be in error with respect to several features. I refer it to *Arrup* provisionally.
8. *A. pauroporus* (Takakuwa, 1936). (New combination.) Manchuria. See remarks under *doii*.

Composite Description of A. pylorus

INTRODUCTORY: Length—To 22 mm, the majority 15–20 mm. Pedal segments: 41. Body shape: Very slightly attenuate anteriorly; posterior third of body somewhat more strongly attenuate. Color: Body whitish to pale yellowish; head and antennae yellowish-orange. Antenna: Very short and robust; when expanded in Hoyer's mounting medium about twice longer than head. Setae on successive articles gradually increasing in number and decreasing in length. Ultimate article longer than wide; on lateral and mesal surfaces of distal half with short, hyaline, robust setae. Cephalic plate: Only slightly longer than wide (e.g., $l:w = 27:22$). Frontal suture indicated by a weak areolate line. Except for coarsely areolate extreme anterior margin entire dorsal surface very weakly areolate. Shape: Sides slightly incurved, posteriorly weakly convergent; anterior margin projecting forward in a strong angle. Setae long and very robust.

CLYPEUS: Anterocentral fenestra absent. Paraclypeal sutures complete, anteriorly slightly sinuous. Prelabral plagulae* less than half as long as entire clypeus, the plagulae separated by a distinct midlongitudinal areolate strip, entirely without setae. Setae of areolate (anterior) clypeus* disposed essentially in three groups, one central and one on each side. BUCCA: Ventrally without setae. Mesally adjacent to stilus* with a large, triangular, non-areolate area, this bordered anteriorly and laterally by areas of conspicuous areolation. Stilus weak. Spiculum* absent. LABRUM: Midpiece pear-shaped, long, anteriorly very wide. Sidepieces without setae or filaments on posterior edges of posterior alae.* FIRST MAXILLAE: Coxosternum very deep anteroposteriorly; midlongitudinally not suturate, not divided, rarely infolded. Medial lobes and telopodites each hyaline distally and basally separated from coxosternum by distinct suture. SECOND MAXILLAE: Isthmus centrally (*in situ*) broadly membranous and hyaline, not areolate, or the hyaline membrane deeply infolded; the two coxosternites thus in effect separated. Meta-

* I use here a number of terms which I presented as new in 1959 (p. 192). They will be identified by an asterisk and defined again at the conclusion of this paper. By prelabral plagulae I mean the "posterior clypeus" of authors.

meric pore opening posteromesally, not laterally, the pore bounded laterally by a long, thin, prominent foraminal process. Telopodite: First article basally with vestigial ventral and dorsal condyles; ultimate article without pretarsus.

PROSTERNUM: Anterior denticles blunt, low, unpigmented. Setae long and robust. PREHENSOR: Denticles: Trochanteroprefemoral proximal denticle entirely absent, the distal denticle long, robust, deeply pigmented; intermediate articles without denticles; tarsungular basal denticle very wide, not pointed, low, weakly pigmented. Dorsal and ventral edges of ungula smooth, not serrulate. Poison calyx very short,² contained within intermediate articles. Poison gland short, ending posteriorly within the trochanteroprefemur. TERGITES: Basal plate and first 3-4 tergites not bisulcate; remaining tergites (except ultimate pedal tergite) weakly bisulcate, the sulci extraordinarily widely separated. Setae robust, stiff, long.

SPIRACLES: All circular. STERNITES: Porefields absent. Each longer than wide. Approximately the first 8 sternites with very short metasternites that telescope shallowly into succeeding sternites.³ Rhachides* represented by shallow midlongitudinal thickened sides; anteriorly not furcate;⁴ on sternites 1-(12-15).

LEGS: First legs only slightly shorter than those succeeding. Setae long, robust, stiff. Pretarsal parungues very short and approximately equal in length.

ULTIMATE PEDAL SEGMENT: Pretergite bilaterally fissate.⁵ Tergite only slightly longer than greatest width; sides slightly excurved, posteriorly not convergent; rear margin evenly rounded. Presternite concealed and completely divided centrally.⁶ Sternite: Strongly triangular; anterior width greater than length; posterior apex rounded and lobate; densely, finely setose. Coxopleuron: laterally not swollen; anteriorly not encroaching upon preceding segment; posteromesally with a prominent, finely setose swelling. Ventrally adjacent to sternite with three large hemogenous pores, laterally (but not dorsally) with notably smaller pores. Leg: in both sexes moderately inflated; about $\frac{1}{4}$ longer than penult leg; with two tarsal articles; pretarsus absent.

POSTPEDAL SEGMENT: Each female gonopod unipartite, semicircular

² This is in notable contrast to the poison calyx of *holstii*, which is extremely long, extending to the base of the trochanteroprefemur and doubling back on itself. This new character, unnoted until now, will prove most useful in distinguishing between species of the genus.

³ In contrast to the majority of mecistocephalids, where the metasternites project very deeply into the succeeding sternites.

⁴ Attems' description, "spitzwinklig gegabelt" (1929: 154), is in error.

⁵ In all mecistocephalids known to me the pretergite of the ultimate pedal segment is conspicuously fissate bilaterally. I submit this as a new family characteristic.

⁶ In all mecistocephalids this presternite is divided centrally; also, the presternite is always present, although it is often concealed beneath the preceding sternite. The genus *Megethumus* has repeatedly been characterized as lacking this presternite, but I have never failed to find it.

in outline, completely but narrowly separated from its counterpart. Male gonopod bipartite, conical in outline, very widely separated from its counterpart. Anal pores opening laterally, very large, their lumina lines with a prominent sclerotic membrane, homogeneous.

Distribution of A. pylorus: The species is known only from California. Type localities: MARIN CO., Sausalito; ALAMEDA CO., Berkeley.

The specimens used in the present study were collected in the following localities: SONOMA CO., west of Mark West Reservation, in Douglas fir litter; SAN MATEO CO., 6 mi. SE Half Moon Bay, in redwood litter, Pescadero Creek, SE Half Moon Bay; MENDOCINO CO., Caspar.

Terminology: Prelabral plagula (of the clypeus). Plagula means flat, smooth place; thereby I refer to the smooth, non-areolate area anterior to each labral sidepiece. There may be two plagulae separated from each other by a midlongitudinal areolate strip (e.g., *Arrup*, *Mecistocephalus*), or a single, undivided plagula that extends nearly to the anterior clypeal margin (e.g., *Tygarrup*, *Dicellophilus*). That portion of the clypeus that is anterior to the plagula(e) may be termed the areolate clypeus or areolate part of the clypeus. By plagula(e) I mean, then, what authors have called the "posterior clypeus," and by *aerolate clypeus* I mean what authors have termed the "anterior clypeus." This older terminology is objectionable, I believe, because it implies a basic, morphological subdivision of the clypeus, which does not in fact exist. Moreover, in genera like *Tygarrup* and *Dicellophilus*, in which the non-areolate area ("posterior clypeus" of authors) occupies virtually the entire clypeal area, the older terminology is most confusing and misleading. The terminology that I propose is neutral and merely descriptive, implying nothing about the basic morphological construction of the clypeus.

SPICULUM (of the bucca): Plural, spicula. In Mecistocephalidae, the pigmented spikelike point on the anterior corner of the bucca. It occurs in three genera: *Mecistocephalus*, *Megethmus*, and *Takashimaia*.

Stilus (of the bucca): Plural, stili. The heavily sclerotized, elongate, thickened mesal edge of the bucca; at midlength giving attachment to the maxillae.

Rhachis (or *rachis*): Plural, rhachides. In Mecistocephalidae the elongate, midlongitudinal sternal thickenings or apodemes. Anteriorly the rhachis is bifurcate or not. In its most simple form it may be a deep sulcus with thickened walls (*Arrup*), but in its more developed, complex state it assumes the form of a rodlike apodeme (*Mecistocephalus*).

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